

## Research Article

**Environmental related variation in growth and life-history traits of non-native sailfin catfishes (*Pterygoplichthys* spp.) across river basins of South China**Hui Wei<sup>1,\*</sup>, Fei Liu<sup>1,#</sup>, Lorenzo Vilizzi<sup>2</sup>, Louisa E. Wood<sup>3,4</sup>, Yinchang Hu<sup>1</sup> and Gordon H. Copp<sup>2,5,6</sup><sup>1</sup>Key Laboratory of Recreational Fisheries (Ministry of Agriculture and Rural Affairs), Pearl River Fisheries Research Institute, Chinese Academy of Fisheries Science, Guangzhou, China<sup>2</sup>Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Lodz, Lodz, Poland<sup>3</sup>Centre for Environment, Fisheries and Aquaculture Science, Weymouth, Dorset, UK<sup>4</sup>Centre for Blue Governance, University of Portsmouth, Portsmouth, UK<sup>5</sup>Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk, UK<sup>6</sup>Centre for Ecology, Environment & Sustainability, Bournemouth University, Poole, Dorset, UK; and Environmental & Life Sciences Graduate Program, Trent University, Peterborough, Ontario, Canada

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**OPEN ACCESS****Abstract**

Plasticity in growth and life-history traits is an important attribute of non-native (NN) fishes, facilitating their adaptation to novel environments. Few studies have investigated geographical variations in multiple biological traits and the factors affecting the variations. In this study, variations in multiple biological traits of NN sailfin catfishes *Pterygoplichthys* spp. were investigated in the main river basins of the Guangdong and Hainan provinces of South China. The impacts of environmental factors on the biological traits were analysed using general linear modeling and an information-theoretic approach. Among-basin differences in population growth was observed, with richness of competitor fishes negatively affecting growth, maturity and reproductive traits – this suggests biotic resistance was mediated by competition with native fishes. These traits were positively affected by total phosphorus concentration, which is indicative of bottom-up effects, mediated by inorganic nutrients, potentially playing an important role in the invasion success of NN fish. In population level, a bet-hedging strategy was observed in sailfin catfishes under unfavourable environment conditions (e.g. Nangdujiang), whereas a “master-of-some” strategy was found under favourable conditions (e.g. Pearl River Delta and Western Basin). The results suggested that plasticity in multiple biological traits of sailfin catfishes is an important strategy to overcome changing environmental conditions in different rivers, and habitat-specific variations across river basins would reflect trade-offs amongst traits at the population level. Therefore, habitat-specific management measures, adapted to the invaded ecosystem’s features and the life-history strategy of the NN species, could provide an effective means to control invasive species.

**Key words:** fish invasion, phenotypic plasticity, multiple biological traits, resource availability, loricariid fish

**Introduction**

Non-native (NN) species must overcome abiotic and biotic barriers in order to establish and spread into novel environments (Richardson et al. 2000; Warnock and Rasmussen 2013), where they can adapt by shifting their

phenotypic and life-history traits (Davidson et al. 2011). Growth and life-history traits of fish species that are sensitive to environmental changes are known to vary across clines and geographical regions (Copp et al. 2004; Blanck and Lamouroux 2007; Fox and Copp 2014; Wilson et al. 2019), and these traits can be good predictors of the invasiveness of NN fish (Kolar and Lodge 2002). Some invasive fish species have been found to be fast *r*-selected strategists with high plasticity in their life-history traits (Bøhn et al. 2004; Masson et al. 2016). For example, NN pumpkinseed *Lepomis gibbosus* mature earlier and at a smaller size and allocate more energy to reproduction in their areas of introduction than in their native region (Fox and Copp 2014), and the growth rate of their adults has been found to be slower (Copp et al. 2004) and to decrease with latitude with mean age at maturity increasing (Cucherousset et al. 2009). These findings indicate that high plasticity in life-history traits is an important ability for introduced fishes to colonise new environments. However, few studies have explored the mechanisms driving variations in multiple biological traits of NN fish across geographical regions (e.g. Jia et al. 2019).

Temperature, precipitation, resource availability and biotic interactions (i.e. competitors and predators) are key factors affecting the growth, maturity and reproduction of fish species (Stearns 1977; Winemiller 1989). These abiotic and biotic factors vary among some species' native and introduced regions, and also within the latter (Fox and Copp 2014; Davidson et al. 2011). Despite evidence that invasive fish species are generally larger relative to their native counterparts (Blanchet et al. 2010), a recent meta-analysis study indicated that invasive freshwater fish populations do not always grow faster due to covariates including climate and counter-gradient growth variation (Rypel 2014). The aforementioned meta-analysis is supported by the considerable evidence for smaller size of introduced pumpkinseed than native populations (Copp et al. 2004; Fox and Copp 2014). Moreover, human-mediated environmental changes (e.g. eutrophication, climate warming, etc.) substantially affect habitat quality (Smith and Schindler 2009; Diez et al. 2012). And although disturbed communities are generally prone to invasion by NN species due to ecological windows of opportunity created as a result of the losses of native species (Diez et al. 2012), few studies have explored the response of biological traits of NN fish to multiple environmental conditions in their introduced range (e.g. Jia et al. 2019).

Native to South America, loricariid species known as sailfin catfishes, *Pterygoplichthys* spp. (a.k.a. plecos, armoured catfishes or janitor fishes), have been introduced to several tropical and sub-tropical regions worldwide. In many locations, ecological impacts (e.g. disruption of nutrient cycling and food webs) and economic losses (e.g. decrease in the abundance of economically important species and damage to fishing gears) have been attributed to these introduced fishes (review in Orfinger and Goodding 2018). *Pterygoplichthys* species have invaded in the main river basins of

South China (Wei et al. 2017). All occurrences of the species might refer to the hybrid *P. disjunctivus* × *pardalis* in these basins according to morphological traits and preliminary genetic analysis (Wei et al. 2017). Some genetic studies also indicated that morphological and genetic traits between *P. pardalis* and *P. disjunctivus* were homogenised with no differentiation, which suggested these two closely-related species might be synonyms (Jumawan et al. 2011; Wu et al. 2011). Further work is needed to confirm this. Given the uncertainty of the species identification, sailfin catfishes is used to refer to *Pterygoplichthys* spp. in the present study.

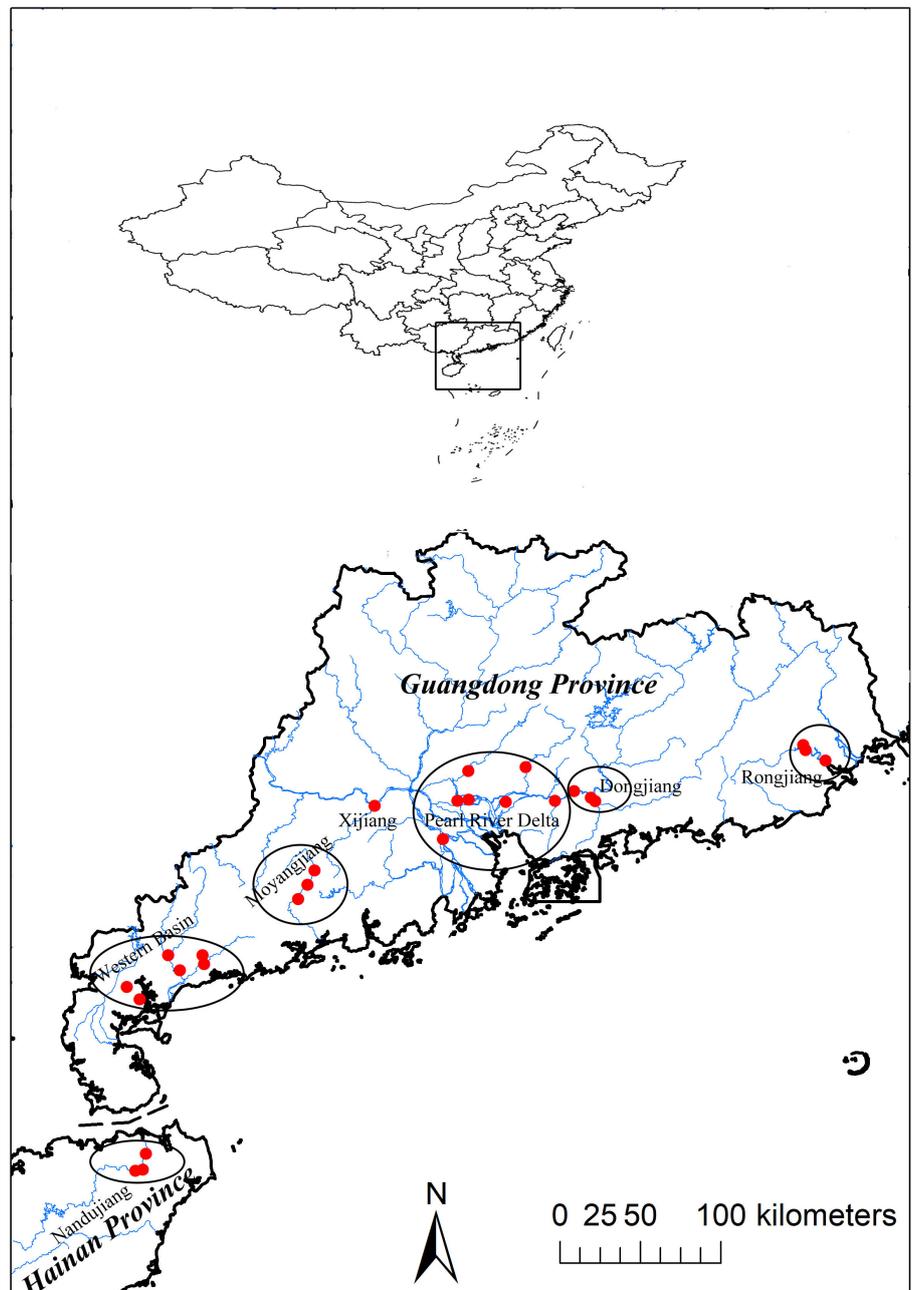
Previous studies have suggested that mean size at maturity of sailfin catfishes varies amongst different river basins (Wei et al. 2017, H. Wei and L.E. Wood *unpublished data*), with reproduction strategies changing over time (Gibbs et al. 2017). However, there is little information available on the factors that drive variations in growth and life-history traits of sailfin catfishes within their introduced regions. The aims of the present study were to: 1) investigate geographical variations in multiple biological traits of sailfin catfishes in the main river basins of South China; and 2) identify the factors affecting such variations. Understanding the mechanisms driving variations in multiple biological traits could help reveal why NN species can be successful invaders of new habitats. In turn, this knowledge would assist decision makers in the implementation of measures for the management of invasive NN fish.

## Materials and methods

### *Study area and sample processing*

Sailfin catfishes were collected from the main basins and a river delta of Guangdong province (21°15'N; 23°3'E) and from the basin Nanduijiang in Hainan province (19°43'N; 19°59'E) (Figure 1, Supplementary material Table S1). Guangdong province is characterised by a sub-tropical monsoon climate with mean winter temperature of 13.4 °C, mean summer temperature of 28.5 °C, and mean annual rainfall of 1790 mm mainly between April and September. Hainan province has a tropical monsoon climate with mean winter temperature of 18 °C, mean summer temperature of 28 °C, and mean annual rainfall of 1670 mm, mainly between May and October (China Weather 2016).

A total of 1799 specimens of sailfin catfishes were collected during summer and early autumn in 2015 and 2016 at a river delta and each of the six river basins in the study area (Figure 1): Dongjiang (DJ), Moyangjiang (MJ), Nanduijiang (NJ), Pearl River Delta (PRD), Rongjiang (RJ), Western Basin (WB) and Xijiang (XJ). Specimens were collected from between one to seven sampling sites within the river delta and each river basin. Between 20 and 50 specimens were collected from each population. Standard length (SL) of each fish was measured (nearest 1 mm), and all specimens were dissected to remove gonads and livers. Total weight ( $W_t$ ), eviscerated weight



**Figure 1.** Sampling locations for sailfin catfishes *Pterygoplichthys* spp. in the main river basins of Guangdong and Hainan Provinces of China.

( $W_e$ ), gonad weight ( $W_g$ ) and liver weight ( $W_l$ ) were measured (nearest 0.01 g). The left ovary was weighed ( $W_o$ ) and the number of eggs ( $N_e$ ) counted from which 100 eggs were randomly selected for measurement of their diameter (nearest 0.01 mm) to determine egg size (ES). These selected eggs contained small and large eggs. Lapillus otoliths were retrieved from each fish and polished to enhance visibility of growth bands. Age was estimated by counting growth band pairs (i.e. translucent and opaque zones: after Gibbs et al. 2013), and all otoliths were read three times by the first author under a microscope (OLYMPUS CX 41). Precision of age estimates was computed after Gibbs et al. (2013). The mean estimated age ( $t$ ) of each specimen was then used in further analysis.

### *Biological traits and environmental factors*

The following biological traits were computed:

1. Mean age at maturity (DeMaster 1978) as adapted by Fox (1994):  $AGE_M = \sum_{t_0}^t (t)P(t)$ , where  $t$  is the maximum age in the samples and  $P(t)$  is the estimated probability of first spawning at age  $t$  (calculated also separately for males and females:  $MAGE_M$  and  $FAGE_M$ );
2. Mean size at maturity, using the Trippel and Harvey (1987) adaptation of the DeMaster (1978) formula given here above:  $SL_M = \sum_{SL_0=0}^{SL} (SL)P(SL)$ , where  $SL$  is the maximum standard length in the samples and  $P(SL)$  is the estimated probability of first spawning at length  $SL$  (calculated also separately for males and females:  $MSL_M$  and  $FSL_M$ );
3. Relative growth of the liver, based on the hepatosomatic index:  $HSI = 100 \times W_L/W_p$ , calculated from mature individuals;
4. Absolute fecundity:  $AF = (W_g/W_o) \times N_e$ ;
5. Relative fecundity:  $RF = AF/W_e$ ;
6. Relative growth of the gonads, using the gonado-somatic index:  $GSI = (W_g/W_e) \times 100$ , calculated from mature females;
7. Mean egg size ( $ES_M$ ) for each matured female.
8. Variability in egg size ( $ES_{CV}$ ) computed both within and among females using the coefficient of variation ( $CV = SD/\text{mean} \times 100$ : Morrongiello et al. 2012).
9. Bioenergetic expression of fish growth based on age using the von Bertalanffy growth function (VBGF) parameters, which are estimated from the equation:  $SL_t = SL_\infty (1 - e^{-K(t-t_0)})$ , where  $SL_\infty$  is the asymptotic  $SL$ ,  $K$  is the Brody growth coefficient ( $\text{years}^{-1}$ ) and  $t_0$  is the age of the fish at 0 mm  $SL$ ;
10. Growth performance using the Pauly and Munro (1984) index:  $\Phi' = \text{Log}K + 2\text{Log}SL_\infty$ ;
11. Mortality rate (Pauly 1980):  $\text{Log}M = -0.0066 - 0.279\text{Log}SL_\infty + 0.6543\text{Log}K + 0.4634\text{Log}T$ , where  $T$  is the mean annual water temperature.

In total, seven environmental factors were measured: Predators, Competitors, Total Phosphorus, Total Nitrogen, Invasion history, Water temperature, Rainfall. The richness of Predators and of Competitors in each basin was estimated based on the peer-reviewed literature, which documented the fish species in the basins based on the surveys in the Guangdong and Hainan Province (see Appendix 1 for the references). Whilst most of the Predators and Competitors considered in the present study were native, NN fish Predators and Competitors ( $n = 10$ ) were also counted. Three water samples were collected in the sampled river sections. *In situ* concentration of Total Phosphorus was measured as  $\text{PO}_4^{3-}$  by the ammonium molybdate method and of Total Nitrogen as  $\text{NO}_3^-$  by ultraviolet

spectrophotometry (SEPA and Editorial Board of Water and Wastewater Monitoring and Analysis Methods 2002). Invasion history (in years present in each river basin) was estimated by consulting local fishers. Water temperature was calculated after Preud'homme and Stefan (1992) as:  $T = 5 + 0.75T_a$ , where  $T_a$  is air temperature. Air temperature and Rainfall data were collected from the China Meteorological Data Service Center (2018) and measured as mean annual values (estimated by data from 1980–2010), with the additional computation of Water temperature variation (difference between highest and lowest annual temperature).

### Statistical analyses

Differences in  $AGE_M$ ,  $SL_M$  and HSI between basins and sex were investigated separately by permutational univariate analysis of variance (permutational ANOVA) based on a two-way design (Basin and Sex), and differences in AF, RF, GSI,  $ES_M$ ,  $ES_{CV}$  between basins jointly by permutational multivariate analysis of variance (permutational MANOVA) based on a one-way design (Basin), with factor Basin random in both designs and Sex fixed. Analyses were carried out in PRIMER v7, with Log-transformation of AF and GSI, normalisation of the data, using Bray-Curtis dissimilarity measure, 9999 unrestricted permutations of the raw data, and with statistical effects evaluated at  $\alpha = 0.05$ .

Following Vilizzi and Copp (2017), VBGF-based comparisons in growth of sailfin catfishes amongst basins were made by fitting eight models in total: i) a general model with separate parameter estimates for each population ( $SL_{\infty DJ} \neq SL_{\infty MJ} \neq SL_{\infty NJ} \neq SL_{\infty PRD} \neq SL_{\infty RJ} \neq SL_{\infty WB} \neq SL_{\infty XJ}$ ,  $K_{DJ} \neq K_{MJ} \neq K_{NJ} \neq K_{PRD} \neq K_{RJ} \neq K_{WB} \neq K_{XJ}$ ,  $t_{0DJ} \neq t_{0MJ} \neq t_{0NJ} \neq t_{0PRD} \neq t_{0RJ} \neq t_{0WB} \neq t_{0XJ}$ ; basin abbreviations as above); ii) three models with one parameter in common amongst population ( $SL_{\infty}$ ,  $K_{DJ} \neq \dots K_{XJ}$ ,  $t_{0DJ} \neq \dots t_{0XJ}$ ;  $SL_{\infty DJ} \neq \dots SL_{\infty XJ}$ ,  $K$ ,  $t_{0DJ} \dots t_{0XJ}$ ;  $SL_{\infty DJ} \neq \dots SL_{\infty XJ}$ ,  $K_{DJ} \neq \dots K_{XJ}$ ,  $t_0$ ); iii) three models with two parameters in common amongst populations ( $SL_{\infty}$ ,  $K$ ,  $t_{0DJ} \neq \dots t_{0XJ}$ ;  $SL_{\infty}$ ,  $K_{DJ} \neq \dots K_{XJ}$ ,  $t_0$ ;  $SL_{\infty DJ} \neq \dots SL_{\infty XJ}$ ,  $K$ ,  $t_0$ ); and iv) one common model with the same parameter estimates for all populations ( $SL_{\infty}$ ,  $K$ ,  $t_0$ ). Both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) were computed to select the best-fitting model, with preference given to BIC in case of major disparity of outcomes for reasons of model parsimony (i.e. fewer parameters), otherwise to AIC for “biological meaningfulness” (Burnham and Anderson 2003). Following model selection, the Gallucci-Quinn (G-Q) parameterisation of the VBGF (Gallucci and Quinn 1979) was used for growth comparison amongst basins based on parameter  $\omega = KSL_{\infty}$ , which has been shown to capture essential features of growth in fish effectively (Živkov et al. 1999; Charnov 2010), where the  $SL_{\infty}$  predicted by the model approximates observed maximum sizes for the species as well as facilitate comparisons among populations (Ogle 2016). Fitting of models was in R v3.6.3 (R Development Core Team 2020) using

packages “FSA” and “nlstools” (Ogle 2016) with 1000 bootstrap confidence interval estimates of the parameters (and with additional code written by LV). Relationships between  $\omega$  and the environmental factors were assessed qualitatively by scatterplots with superimposed moving average trendline of period 2.

General linear modelling combined with an information-theoretic approach was used to select the “best” model explaining the relationship of environmental factors on variations in biological traits. Collinearity was checked using the variance inflation factor (VIF), and using a cut-off value of two as a sign of collinearity as per Zuur et al. (2010). Analysis was in R with general linear models fitted with package MASS. Exhaustive screening of candidate sets of models was carried out with package glmulti (Calcagno and deMazancourt 2010), using all combinations of the main terms (63 candidate models in total). The “best” models were then selected based on log-likelihood and second order Akaike’s information criterion (AICc) for small sample size, with a minimum  $\Delta\text{AICc} < 2$  indicating difference between the current model and minimum AICc (Burnham and Anderson 2002). Akaike’s model weight ( $\omega_i$ ) and the adjusted coefficient of determination  $R^2$  were then used to evaluate the importance of the selected models. Given the uncertainty in model selection, package MuMIn (Barto’n 2019) was used to calculate average model parameters ( $\beta$ -value), unconditional standard errors (unconditional SE), unconditional 95% confidence intervals and variable-specific importance values based on AICc weights.

## Results

There were statistically significant differences amongst basins in the four biological traits examined (Table 1, Figure 2). A VBGF with separate (i.e. basin-specific) parameter estimates for  $K$  and with a common  $\text{SL}_\infty$  and  $t_0$  was selected based on both AIC and BIC and for biological meaningfulness (Table 2). Parameter estimates were then computed for the corresponding G-Q parameterisation yielding corresponding  $\omega$  values (Table 2). Based on these, sailfin catfishes grew faster and to a larger size in the river basins Western Basin and Pearl River Delta, and slower and at a smaller size in the river basins Moyangjiang, Xijiang and Nandujiang, with “intermediate” growth in the river basins Rongjiang and Dongjiang (Figure 3). Overall, there was an indication for parameter  $\omega$  to increase with a decrease in richness of predators and to increase, to some extent, with Total Phosphorus and years of invasion history (Figure 4).

In the best-fit models for male and female  $\text{AGE}_M$  and  $\text{SL}_M$ , the main drivers of variations (i.e. environmental factors) included Competitors, Water Temperature and, to some extent, Total Phosphorus (Tables 3 and 4; see also Tables S2 and S3). Competitors negatively affected  $\text{AGE}_M$  (males only) and  $\text{SL}_M$ , whereas Total Phosphorus and Water Temperature had a

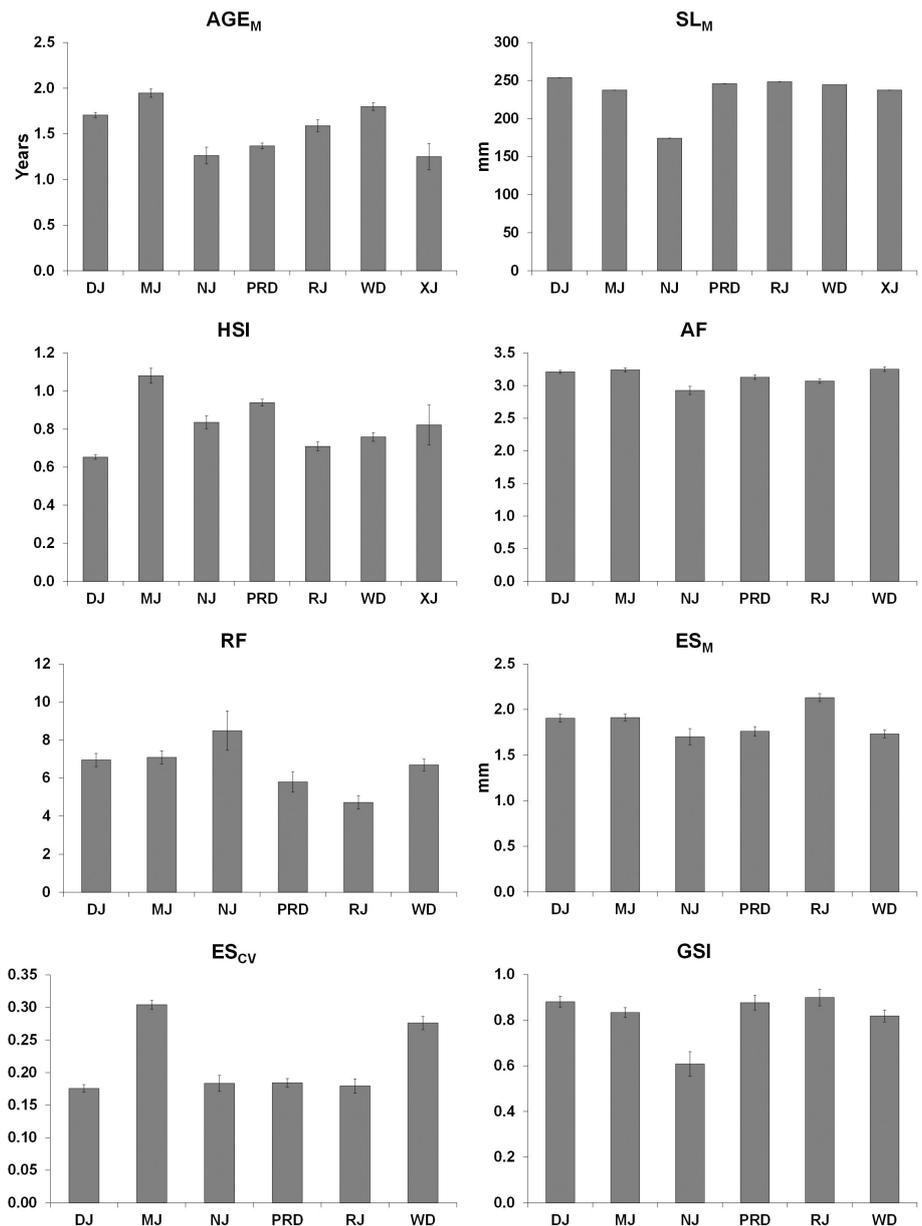
**Table 1.** Permutational ANOVA ( $AGE_M$ ,  $SL_M$ , HSI) and permutational MANOVA (“reproductive traits”: AF, RF, GSI,  $ES_M$ ,  $ES_{CV}$ ) results for differences between river basins and sex for sailfin catfishes *Pterygoplichthys* spp. in South China (see text for variable description). Statistically significant effects ( $\alpha = 0.05$ ) in bold. # = permutational value.

Source of variation	df	MS	$F^\# / t^\#$	$P^\#$
$AGE_M$				
Basin	6	15.26	18.43	< <b>0.001</b>
Sex	1	0.02	0.03	0.876
Basin $\times$ Sex	6	1.42	1.71	0.124
Residual	667	0.83		
$SL_M$				
Basin	6	24.84	14.24	< <b>0.001</b>
Sex	1	1.10	0.58	0.564
Basin $\times$ Sex	6	2.54	1.45	0.152
Residual	667	1.74		
HSI				
Basin	6	25.77	31.67	< <b>0.001</b>
Sex	1	3.97	3.01	0.151
Basin $\times$ Sex	6	2.31	2.84	<b>0.013</b>
Residual	1095			
Reproductive traits				
Basin	5	39.24	8.99	< <b>0.001</b>
Residual	270	4.36		

positive effect on  $FSL_M$ , and  $FAGE_M$  was also positively affected by Water Temperature variation. Rainfall had a positive effect on HSI. In terms of reproductive allocation (Tables 3 and 4; see also Tables S2 and S3), AF and GSI were both negatively affected by Competitors, whereas Rainfall and Total Phosphorus had a positive effect on RF, Water temperature on GSI. For growth parameters (Tables 3 and 4; see also Tables S2 and S3), Competitors also negatively affected both  $SL_\infty$  and  $\Phi'$ . Water temperature had a positive effect on the  $SL_\infty$ . Predators and Total Phosphorus positively affect  $SL_\infty$  and  $\Phi'$ , which was also negatively affected by Water temperature variation. Water temperature had a positive effect on M. Finally, there were no statistically significant relationships between the environmental factors and  $ES_M$ ,  $ES_{CV}$  or the K growth coefficient.

## Discussion

In the present study, geographical variations in biological traits were identified as described by age and size at maturity, HSI, growth and reproductive traits, suggesting plasticity in the introduced sailfin catfishes. These variations could be explained by the climate characteristics, richness of fish competitors and predators, and nutrient availability of the invaded river basins. Species diversity in native communities could represent a factor of resistance to invasions by NN species due to limited total resource availability (Davis et al. 2000; Levine et al. 2004). Therefore in some cases, newly-introduced species may not be able to persist in the community due to high competition from native species for resources (Levine et al. 2004). The results of the present study suggest that the increase in richness of omnivorous fish species could decrease growth, fecundity, maturity and reproductive allocation in sailfin catfishes. However, the increase in richness of piscivorous fish species could increase their growth performance, as

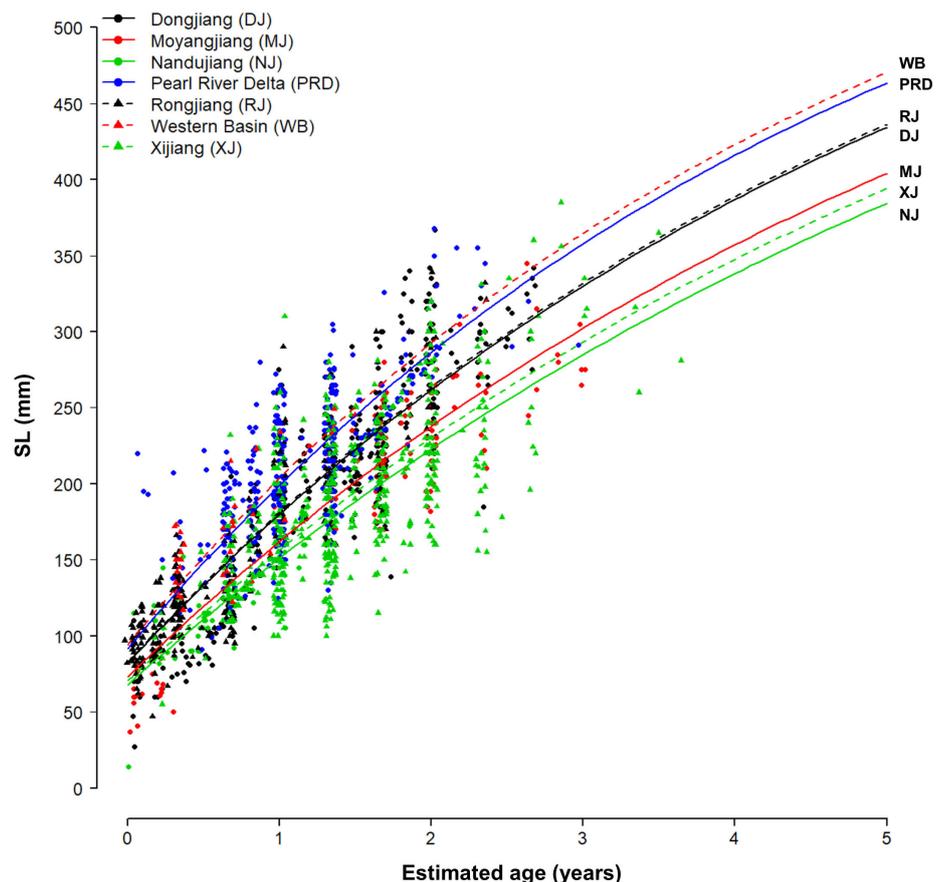


**Figure 2.** Spatial variations of biological traits of sailfin catfishes across the main river basins of South China. Biological traits: AGE<sub>M</sub> = mean age at maturity; SL<sub>M</sub> = mean size at maturity; HSI = hepatosomatic index; AF = absolute fecundity; RF = relative fecundity; ES<sub>M</sub> = mean egg size; ES<sub>CV</sub> = variability in egg size; GSI = gonado-somatic index. River basins: DJ = Dongjiang; MJ = Moyangjiang; NJ = Nandujiang; PRD = Pearl River Delta; RJ = Rongjiang; WD = Western Basin; XJ = Xijiang.

predators have been reported to affect resource allocation between growth and reproduction (i.e. Riessen 1999; Fox and Copp 2014). The present study also demonstrated a weak negative influence of the richness of predators on mean age at maturity and a positive impact on mean size at maturity of sailfin catfishes. In this regard, fish species may allocate more energy to growth to achieve a large size in a short time period in order to avoid predation by piscivorous fish (Riessen 1999). Although biotic resistance in freshwater ecosystems is mainly driven by consumers (Alofs and Jackson 2014), the present study is an exception in that resistance results from competition with native fishes.

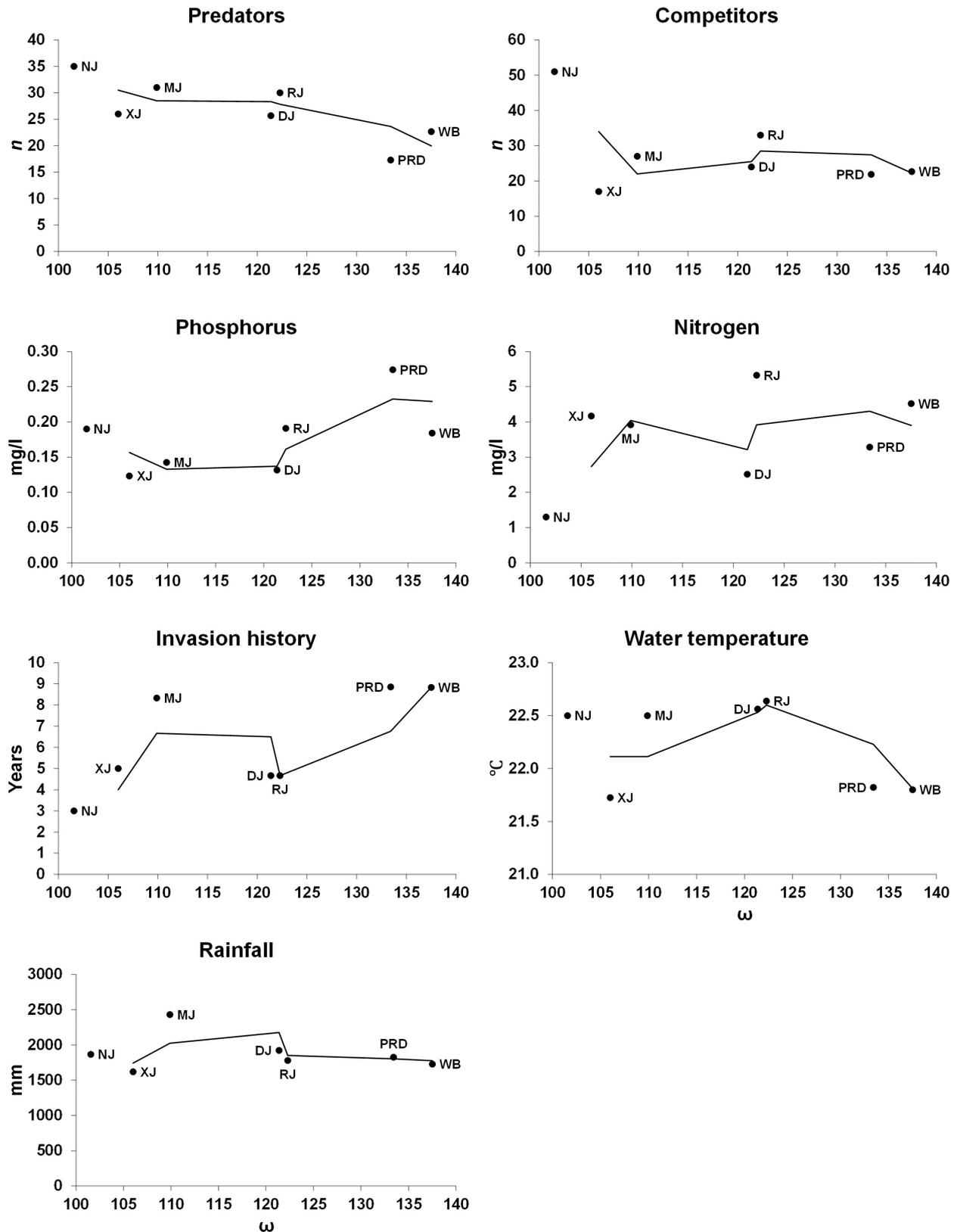
**Table 2.** Growth of sailfin catfishes *Pterygoplichthys* spp. from seven river basins (abbreviations in Figure 1) of South China (Figure 1) as described by the von Bertalanffy growth function (VBGF). For each “best fitting” model, parameter estimates are provided including  $\pm$ SE (standard error) and 95% LCI and UCI (lower and upper confidence intervals, based on 1000 bootstrap iterations). VBGF parameters:  $SL_{\infty}$  = asymptotic standard length (mm);  $K$  = Brody growth coefficient ( $\text{years}^{-1}$ );  $t_0$  = age of fish at 0 mm;  $\omega = KSL_{\infty}$ . See also Figure 2.

Parameter	Estimate	$\pm$ SE	LCI	UCI	$t$	$P$
$SL_{\infty}$	673.0	116.1	518.2	1088.6	5.80	< 0.001
$K_{DJ}$	0.18	0.04	0.10	0.27	4.12	< 0.001
$K_{MJ}$	0.16	0.04	0.09	0.24	4.15	< 0.001
$K_{NJ}$	0.15	0.04	0.08	0.22	4.20	< 0.001
$K_{PRD}$	0.20	0.05	0.11	0.30	4.06	< 0.001
$K_{RJ}$	0.18	0.05	0.10	0.27	4.05	< 0.001
$K_{WB}$	0.21	0.05	0.11	0.32	3.99	< 0.001
$K_{XJ}$	0.15	0.04	0.08	0.23	4.23	< 0.001
$t_0$	-0.72	0.07	-0.87	-0.60	5.80	< 0.001
$\omega_{DJ}$	121.4	8.3	103.2	137.1	14.69	< 0.001
$\omega_{MJ}$	109.9	7.9	92.6	124.4	13.97	< 0.001
$\omega_{NJ}$	101.6	7.4	86.2	115.5	13.70	< 0.001
$\omega_{PRD}$	133.4	9.0	112.5	149.7	14.90	< 0.001
$\omega_{RJ}$	122.3	8.9	103.5	138.6	13.73	< 0.001
$\omega_{WB}$	137.5	10.6	114.6	155.7	12.94	< 0.001
$\omega_{XJ}$	106.0	7.3	89.6	118.9	14.56	< 0.001



**Figure 3.** The relationships in sailfin catfishes between estimated age and body length based on the von Bertalanffy growth function across basins.

Resource availability in a community is a well-known important factor that could influence the invasion success of NN species (Davis et al. 2000). Invasive NN species generally exhibit higher resource use efficiency than



**Figure 4.** Relationships in sailfin catfishes between growth parameter  $\omega = KSL_{\infty}$  and the environmental factors assessed qualitatively by scatterplots with superimposed moving average trendline of period 2. Abbreviations of environmental factors and river basins are given in Table 3.

native species, thus benefitting from resource pulses in the community (Funk and Vitousek 2007). This is exemplified by loricariid species, such as

**Table 3.** Environmental factors explaining variations in biological traits of sailfin catfishes *Pterygoplichthys* spp. (see also Table 4). For each life-history trait, the “best” general linear model is provided. Statistics: logLik = Log-likelihood ratio; AICc = Akaike’s information criterion (for small sample sizes);  $\omega_i$  = Akaike’s model weight; Adj.  $R^2 = R^2$  adjusted for the number of predictors in the model. Life-history traits (see text for explanation):  $MAGE_M$  = male mean age at maturity;  $FAGE_M$  = female mean age at maturity;  $MSL_M$  = male mean size at maturity;  $FSL_M$  = female mean size at maturity; HSI = hepatosomatic index; AF = absolute fecundity; RF = relative fecundity; GSI = gonado-somatic index;  $SL_\infty$  = asymptotic SL;  $\Phi'$  = index of growth performance; M = mortality rate; Environmental factors (see text for explanation): Comp = richness of fish competitors; Pred = richness of fish predators; Rain = mean annual rainfall; TP = total phosphorus concentration; WT = mean annual water temperature;  $\Delta T$  = water temperature variation between the highest and the lowest annual temperature.

Life-history trait	Environmental factor	df	logLik	AICc	$\omega_i$	Adj. $R^2$
$MAGE_M$	Comp	3	-10.97	29.04	0.16	0.08
$FAGE_M$	Log $\Delta T$	3	-4.43	15.96	0.10	0.10
$MSL_M$	Comp	3	-129.34	265.78	0.17	0.20
$FSL_M$	Comp, LogTP, LogWT	5	-114.75	242.50	0.20	0.48
HSI	Rain	3	12.18	-17.26	0.26	0.14
Log(AF)	Comp	3	8.93	-10.76	0.12	0.05
RF	Rain, LogTP	4	-46.58	103.06	0.18	0.22
GSI	Comp, LogWT	4	-59.89	129.69	0.24	0.22
$SL_\infty$	LogPred, Comp, LogTP, logWT, Log $\Delta T$	4	-143.96	308.14	0.21	0.48
$\Phi'$	Comp, LogPred, LogTP, Log $\Delta T$	6	21.96	-27.5	0.38	0.38
M	LogWT	3	-23.10	53.29	0.15	0.10

**Table 4.** Biological traits of sailfin catfishes *Pterygoplichthys* spp. responses (+ = positive; - = negative; 0 = null) to environmental factors (see Table 3).  $ED_M$  = mean egg size;  $ED_{CV\_within}$  = variability in egg size within females;  $ED_{CV\_among}$  = variability in egg size among females;  $K$  = Brody growth coefficient (see text for explanation) (all other abbreviations as in Table 3).

Life-history trait	Comp	LogPred	Rain	LogTP	LogWT	log $\Delta T$
$MAGE_M$	-	0	0	0	0	0
$FAGE_M$	0	0	0	0	0	+
$MSL_M$	-	0	0	0	0	0
$FSL_M$	-	0	0	+	+	0
HSI	0	0	+	0	0	0
Log(AF)	-	0	0	0	0	0
RF	0	0	+	+	0	0
GSI	-	0	0	0	+	0
$ES_M$	0	0	0	0	0	0
$ES_{CV\_within}$	0	0	0	0	0	0
$ES_{CV\_among}$	0	0	0	0	0	0
$K$	0	0	0	0	0	0
$SL_\infty$	-	+	0	+	+	-
$\Phi'$	-	+	0	+	0	-
M	0	0	0	0	+	0

sailfin catfishes, which are characterised by high body phosphorus content, hence likely to demand higher amounts of phosphorus in the habitat relative to native species (Hood et al. 2005; Capps and Flecker 2013). Additionally, loricariid females may be more sensitive to increases in phosphorus availability due to their high nutrient demand for the development of reproductive cells (Craik and Harvey 1984). This hypothesis could explain the positive effect of Total Phosphorus (in the river basins of the present study) on female size, relative fecundity, asymptotic length and growth performance in sailfin catfishes. As such, rivers worldwide are faced with increases in human-induced nutrient loading, which have knock-on effects on aquatic community structure (Glibert et al. 2011). Also, increases in extreme rainfall events under climate change scenarios could enhance the transport of nutrients from terrestrial to riverine

ecosystems (Andersen et al. 2006). As a result, those NN species able to tolerate hypoxia (see Armbruster 1998) may benefit from such nutrient increase in rivers because of changes in community structure, with resource pulses providing windows of opportunity for their establishment and spread in newly colonised habitats. This suggests that with loricariid species introductions, a bottom-up mechanism, mediated by inorganic nutrient input in the aquatic ecosystem, appears to play an important role in invasion success.

Temperature is a key factor known to affect species distributions at large geographical scales (Bae et al. 2018), though it is not always a “stable” variable in models of fish responses to environmental variables (Fox and Copp 2014). Temperature can influence species fitness both indirectly, at the ecosystem level, and directly by affecting ontogeny, reproduction and metabolism (Pankhurst and King 2010; Neuheimer et al. 2011). Also, there is a limit on temperature-induced fish growth in that growth decreases with increasing temperature at the warmer extent of a species’ distribution (Neuheimer et al. 2011). Annual temperature variation can also affect fish growth, although fish species can adapt by changing their feeding behaviour (Guzzo et al. 2017). The results from the present study indicated that annual water temperature variation had a negative effect on the growth performance of sailfin catfishes, whereas an increase in mean annual water temperature increased growth and reproductive allocation, but also mortality. These results indicate that sailfin catfishes can adjust its life-history strategy to adapt to temperature variation in habitats it colonises.

Variations in multiple biological traits are important predictors of the persistence or extinction of a population under changing environmental conditions (Dunlop et al. 2009; Martone and Micheli 2012). In the present study, growth and (growth-related) maturity in sailfin catfishes were more sensitive than reproductive traits to environmental changes. Environmental changes affect juvenile fish growth and maturity, with reproductive traits potentially affected by growth compensation in later stages of development under environmental pressure (Wilson et al. 2019). Moreover, the trade-off between allocations to somatic and gonadal growth is important for life-history strategies in response to environmental stochasticity (Dunlop et al. 2009). For example, somatic growth and age at maturity of lake trout *Salvelinus namaycush* were significantly affected by exploitation, climate, and resources supplies, whereas reproductive allocation was affected by evolutionary trade-offs with mortality and other life-history traits (Wilson et al. 2019).

The “phenotypic hypothesis” purports that species employ “jack-and-master” strategies in their phenotypical traits to increase fitness in order to adapt to changing environmental conditions (Richards et al. 2006). Thus, species can exhibit phenotypical traits to maintain fitness in adverse environments, i.e. jack-of-all-trades or conservative bet-hedging) (Starrfelt

and Kokko 2012; Scheiner 2014), whilst displaying phenotypes to increase fitness in favourable environments (master-of-some). Alternatively, a species may employ both strategies in order to maximise fitness in stochastic environments (jack-and-master). The observed variations in multiple biological traits of sailfin catfishes across different river basins can be explained using the above hypothesis. Accordingly, variations in life-history traits reflected a bet-hedging strategy with a decrease in fitness (i.e. slow growth rate, low reproductive allocation, etc.) in unfavourable environments (e.g. basin Nanduijiang). This is consistent with a jack-of-all-trades strategy, whereby sailfin catfishes appear able to maintain fitness in adverse environments due to the plasticity of their phenotypic traits. This is in contrast to more favourable environments (e.g. Pearl River Delta and Western Basin) characterised by a relative low richness of fish predators and competitors, higher temperature, nutrient availability and longer history of sailfin catfish introduction, hence consistent with a master-of-some strategy. These results also suggested that, relative to response to single environmental factors, life-history traits responded differently to multiple environmental factors (i.e. Jia et al. 2019). In this regard, the former could better reflect the adaptive responses of sailfin catfishes to a combination of multiple environmental factors in their colonised habitat.

### Implications for management

Non-native fish invasions can result in biodiversity losses of native species, habitat alteration, and changes in food web structure (Gallardo et al. 2015; Bajer et al. 2016). Understanding the ecological processes leading to successful fish invasions will help to implement appropriate measures for management and control. In the present study, variation in multiple biological traits of sailfin catfishes could be explained by the climate characteristics, richness of competitors and predators, and nutrient availability across river basins. The plasticity in these traits was driven by trade-offs in basin-specific environmental conditions (hence, at the population level). Most sailfin catfishes in the main river basins of South China have experienced a genetic bottleneck (Fu's neutrality test:  $F_s > 0$ ; H. Wei and L.E. Wood *unpublished data*) and some populations have adopted a bet-hedging strategy in their newly-colonised habitats. Additionally, inter-population variations and trade-offs amongst biological traits can be used to distinguish the invasiveness of NN fish in different populations (Fox 1994; Copp and Fox 2007, 2021). In the present study, sailfin catfishes in basins Moyangjiang, Nanduijiang and Xijiang, where they displayed slower growth, smaller ultimate size and earlier maturity, could be considered as "non-invasive" (or less invasive) relative to populations in other basins, whereas populations in basins the Pearl River Delta and the Western Basin, which matured early and grew faster and to a larger size, might be more invasive (e.g. Copp and Fox 2021). These findings suggest that measures

for management and control of these NN fishes can be developed to minimise the worst effects of the NN fishes at this stage. For example, conservation and restoration of the diversity of competitor species in the invaded water bodies may lead to reduced growth and reproduction of NN sailfin catfishes, but this would require further, detailed investigation. Also, ecosystem-based nutrient management strategies might also help to maintain native fish and control the invasive NN fish.

The observed plasticity in multiple biological traits of sailfin catfishes is an important strategy to overcome changing environmental conditions in different rivers, and habitat-specific variations across river basins would reflect trade-offs amongst traits at the population level. The present findings indicate that habitat-specific management measures could be more effective in the control of invasive species when based on their life history strategies (e.g. Kolar et al. 2010). Further studies are also needed to evaluate the response of multiple biological traits of introduced and native species to global environmental changes at large and small spatial scales. This would provide knowledge on whether NN species would always take advantage of these conditions, in turn providing more specific information for ecosystem management under global environmental change scenarios.

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### Authors' contributions

Wei H. conceptualised the study, collected and analysed the data and prepared the manuscript; Hu Y. conceptualised the study; Liu F collected the data; Copp G.H., Vilizzi L. and Wood L.E. analysed the data and participated in composing the manuscript.

### Data availability statement

The data that support the findings of this study are available on request from the corresponding author.

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### Supplementary material

The following supplementary material is available for this article:

**Table S1.** Sampling sites and records of sailfin catfishes *Pterygoplichthys* spp. in the main river basins of Guangdong and Hainan Provinces of China.

**Table S2.** Environmental factors explaining variation in life-history traits of sailfin catfishes *Pterygoplichthys* spp.

**Table S3.** Model-averaged parameter estimates ( $\beta$ -value), unconditional standard errors (SE) and 95% lower and upper confidence intervals (LCI and UCI) based on general linear models explaining the life-history traits of sailfin catfishes *Pterygoplichthys* spp.

**Appendix 1.** References of the fish species data in South China.

This material is available as part of online article from:

[http://www.reabic.net/aquaticinvasions/2022/Supplements/AI\\_2022\\_Wei\\_etal\\_SupplementaryMaterial.xlsx](http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Wei_etal_SupplementaryMaterial.xlsx)